

The Effects of Aerial Exposure and Desiccation on the Oxygen Consumption of Intertidal Limpets

by

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Abstract. Aquatic and aerial rates of oxygen consumption were determined for the intertidal prosobranch limpets *Notoacmea pileopsis* and *Cellana radians* at 10°C. Rates of oxygen consumption of the two species did not differ significantly between aquatic and aerial environments. The aerial rates of oxygen uptake of both species decreased significantly after a period of desiccation. The results are discussed with reference to previous reports on the respiration of acmaeid and patellid limpets in air and water.

INTRODUCTION

A FEATURE of the rocky shores of New Zealand is the presence of an acmaeid limpet, *Notoacmea pileopsis* (Hombron & Jacquinot, 1841), in the splash zone (MORTON & MILLER, 1968). Acmaeid limpets retain a primitive aspidobranch gill (PURCHON, 1968) and are more frequently encountered in low shore or subtidal habitats. Previous respiratory studies on intertidal and subtidal acmaeids have reported depressed rates of oxygen consumption during aerial exposure (BALDWIN, 1968; MCMAHON & RUSSELL-HUNTER, 1977). In contrast, patellid limpets, which possess secondary pallial gills, are often found on the upper levels of the shore, and several species appear capable of maintaining aerobic metabolism during emersion (BANNISTER, 1974; BRANCH & NEWELL, 1978; HOULIHAN & NEWTON, 1978; BRANCH, 1979). In the present study, the oxygen consumption of *Notoacmea pileopsis* in water and air is investigated to determine whether this limpet's vertical distribution on the shore is correlated with an enhanced capacity for aerial gas exchange as has been demonstrated for other gastropods (MICALLEF, 1967; MICALLEF & BANNISTER, 1967; MCMAHON & RUSSELL-HUNTER, 1977; HOULIHAN, 1979; HOULIHAN & INNES, 1982a, b). The relationship between aquatic and aerial oxygen uptake is also determined for a common intertidal patellid limpet, *Cellana radians* (Gmelin, 1791), from the same shore. The relative ability of acmaeid and patellid limpets to respire in aquatic and aerial environ-

ments is discussed with respect to their principal organs of gas exchange (MCMAHON & RUSSELL-HUNTER, 1977).

BALDWIN (1968) demonstrated that the aerial oxygen consumption of acmaeid limpets is significantly depressed after a period of desiccation, but no comparable data are available for patellid limpets. In the present study the effects of desiccation on the aerial rates of oxygen consumption of both *Notoacmea pileopsis* and *Cellana radians* have been investigated and the results are discussed in relation to the respiratory structures of each species. Comparisons are made with a number of other intertidal prosobranchs (SANDISON, 1966; BALDWIN, 1968; SHIRLEY *et al.*, 1978).

MATERIALS AND METHODS

This work was carried out at the Portobello Marine Laboratory, New Zealand, between August and October 1982. The prosobranchs investigated in the present study are the acmaeid limpet *Notoacmea pileopsis*, which is distributed in the splash zone, and the patellid limpet *Cellana radians*, which is commonly found in the intertidal zone (MORTON & MILLER, 1968; POWELL, 1979). All experimental animals were collected from Allans Beach, Portobello.

After collection, the snails were held in a running seawater aquarium without access to food for 7 to 9 days prior to experimentation. The aquarium seawater temperature varied between 7 and 10°C and the salinity was relatively constant at 33.5‰. Experiments were carried out at 10°C and the snails were held at the experimental temperature for two hours prior to respirometry commencing. Experiments took place in constant temperature water baths controlled to $\pm 0.1^\circ\text{C}$.

Aerial rates of oxygen consumption were measured us-

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ing constant pressure respirometers described by DAVIES (1966). The limpets were allowed to recover extra-corporeal fluid as described by HOULIHAN & NEWTON (1978) prior to experiments commencing. For desiccation experiments the respirometer bottles containing the snails were placed in desiccation chambers and held in a constant temperature room at 10°C for periods of 1, 4, and 8 h. Silica gel was used as a desiccating agent and relative humidity (RH) was constant at 20%. Aerial respirometry was carried out as described by HOULIHAN *et al.* (1981). The position of the snail in the respirometer was monitored and rates of oxygen consumption calculated for periods when the animal was seen to be inactive. All rates of oxygen consumption have been converted to STP. Some determinations of aerial oxygen consumption for *Notoacmea* were made with up to three similar-sized snails in a respirometer in order to increase the accuracy of the measurements. These data are expressed as mean oxygen consumption for a mean weight animal.

Aquatic oxygen consumption was measured by the closed bottle technique described by HOULIHAN (1979). The limpets were left overnight to attach and settle in the respirometer bottles in running aerated seawater prior to experiments commencing (HOULIHAN & NEWTON, 1978). After the flasks were sealed, the seawater was stirred every 5 min with a magnetic stirrer, and rates of oxygen consumption were calculated only for those animals that remained inactive throughout the experiment. A blank bottle without an animal was run as a control with each set of experiments. The oxygen content of the seawater at the beginning and end of each experiment was determined by the Winkler technique (STRICKLAND & PARSONS, 1972). Oxygen consumption was calculated from the decline in oxygen content of the seawater, the volume of water in the respirometer bottle, and the duration of the experiment. The oxygen content of the seawater in the flask was never allowed to fall below 80% of the saturated value during experiments (INNES, 1982).

At the end of each experiment the limpets were removed from their shells and dried to a constant weight at 65°C.

Measurements of aquatic and aerial (undesiccated) respiration were made on a wide size range of animals in order to establish relationships between dry weight and oxygen consumption. The results were subjected to regression and covariance analysis (SNEDECOR & COCHRAN, 1972) following the procedure of WILSON (1975). The results of regression analysis using data transformed by logarithms to the base 10 are shown in their logarithmic form. The mean dry flesh weight \pm SE of all the *Notoacmea pileopsis* used in these experiments was 42.5 ± 2.5 mg ($n = 46$) while that of the larger *Cellana radians* was 219.6 ± 24.2 mg ($n = 41$). Standard dry flesh weight animals, *Notoacmea pileopsis* (40 mg) and *Cellana radians* (200 mg), were used to calculate ratios of aquatic to aerial oxygen consumption and to describe the effects of desiccation.

Narrow weight ranges of *Notoacmea pileopsis* (30–50

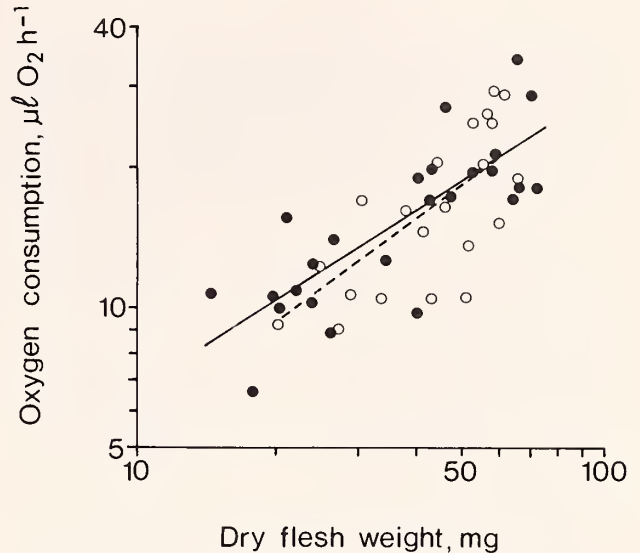


Figure 1

Relationships between dry flesh weight (mg) and oxygen consumption ($\mu\text{L O}_2 \text{ h}^{-1}$) of *Notoacmea pileopsis* in air (\circ — \circ) and seawater (\bullet — \bullet) at 10°C; the lines are drawn from the regression analyses provided in the text.

mg) and *Cellana radians* (160–240 mg) were selected for desiccation experiments. The experimentally determined rates of oxygen consumption of individual animals were transformed to those of standard dry weight *Notoacmea* (40 mg) and *Cellana* (200 mg) using the scaling equation:

$$\dot{V}_{\text{O}_2}(\text{s}) = \left(\frac{W(\text{e})}{W(\text{s})} \right)^b \cdot \dot{V}_{\text{O}_2}(\text{e}) \quad (\text{NEWELL, 1979})$$

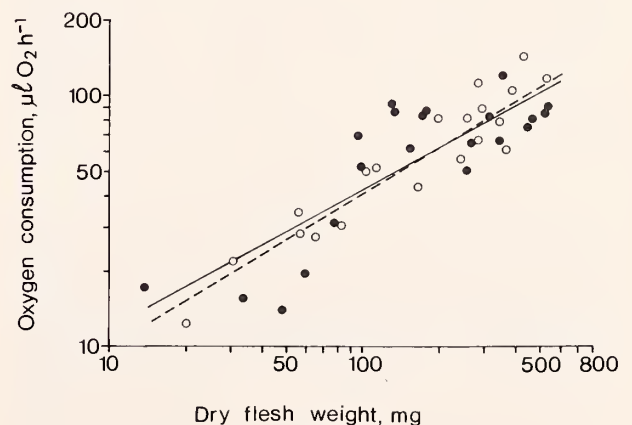


Figure 2

Relationships between dry flesh weight (mg) and oxygen consumption ($\mu\text{L O}_2 \text{ h}^{-1}$) of *Cellana radians* in air (\circ — \circ) and seawater (\bullet — \bullet) at 10°C; the lines are drawn from the regression analyses supplied in the text.

Table 1

Ratios of aquatic oxygen consumption for a number of acmaeid and patellid limpets; ratios have been calculated at the temperatures indicated for standard weight animals using data supplied in the references.

Species	Tem- pera- ture (°C)	Aquatic to aerial ratio	Reference
Acmaeidae:			
<i>Notoacmea pileopsis</i>	10	1:0.95	present study
<i>Collisella scabra</i>	15	1:0.44	BALDWIN (1968)
<i>Collisella digitalis</i>	15	1:0.89	BALDWIN (1968)
<i>Collisella testudinalis</i>	22	1:0.40	MCMAHON & RUSSELL-HUNTER (1977)
Patellidae:			
<i>Cellana radians</i>	10	1:0.97	present study
<i>Patella lusitanica</i>	20	1:3.13	BANNISTER (1974)
<i>Patella caerulea</i>	20	1:0.45	BANNISTER (1974)
<i>Patella oculus</i>	25	1:0.99	BRANCH & NEWELL (1978)
<i>Patella cochlear</i>	25	1:1.04	BRANCH & NEWELL (1978)
<i>Patella granularis</i>	25	1:0.94	BRANCH & NEWELL (1978)
<i>Patella vulgata</i>	10	1:1.41	HOULIHAN & NEWTON (1978)
<i>Patella granatina</i>	25	1:0.99	BRANCH (1979)

where $\dot{V}_{O_2}(s)$ is the calculated rate of oxygen consumption of a standard dry weight animal in $\mu\text{L O}_2 \text{ h}^{-1}$; $W(s)$, the dry flesh weight of a standard animal in mg; $W(e)$, the dry flesh weight of the experimental animal in mg; $\dot{V}_{O_2}(e)$, the experimentally determined oxygen consumption in $\mu\text{L O}_2 \text{ h}^{-1}$; b , the scaling exponent (aerial b values of 0.717 and 0.645 determined for *Notoacmea* and *Cellana* respectively in the present study are used). Statistical comparisons between rates of oxygen consumption under different experimental conditions were made by Students t -test (SNEDECOR & COCHRAN, 1972). Means \pm SE are used throughout.

RESULTS

Oxygen Consumption in Air and Seawater

Rates of oxygen consumption in air and water of a size range of *Notoacmea pileopsis* are presented in Figure 1. The regression analyses describing the relationships between dry flesh weight (X , mg) and oxygen consumption (Y , $\mu\text{L O}_2 \text{ h}^{-1}$) are

Air $\log_{10}Y = 0.717 \log_{10}X + 0.036$, where $n = 21$ and $r = 0.71$.

Seawater $\log_{10}Y = 0.643 \log_{10}X + 0.176$, where $n = 25$ and $r = 0.80$.

The relationships between dry flesh weight and oxygen

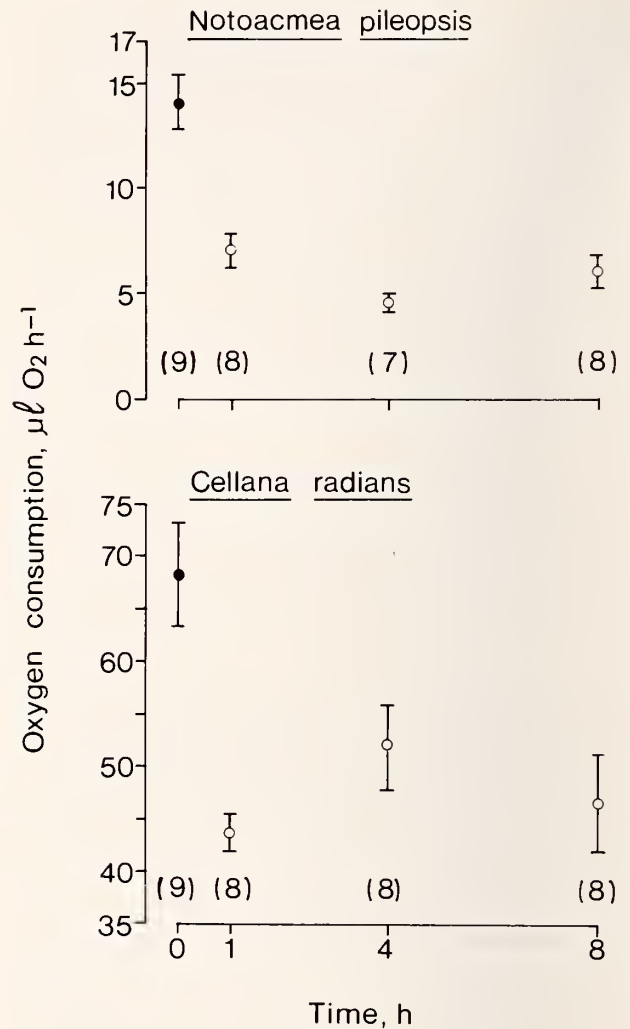


Figure 3

Rates of aerial oxygen consumption ($\mu\text{L O}_2 \text{ h}^{-1}$) \pm SE of standard dry weight *Notoacmea pileopsis* (40 mg) and *Cellana radians* (200 mg) after a brief period of aerial exposure (●) and after 1 h, 4 h, and 8 h desiccation at 20% RH (○); sample sizes (n) are shown in parentheses.

consumption in air and water are both significant ($P < 0.05$). Analysis of covariance showed no significant differences in either slope or elevation between the rates of oxygen consumption of *Notoacmea pileopsis* in aquatic and aerial environments. The ratio of aquatic to aerial oxygen consumption for a standard dry weight animal (40 mg) is 1:0.95 at 10°C.

Aquatic and aerial rates of oxygen consumption of *Cellana radians* are plotted as a function of dry flesh weight in Figure 2. The relationships between dry flesh weight (X , mg) and oxygen consumption (Y , $\mu\text{L O}_2 \text{ h}^{-1}$) are described by the regression analyses

Air $\log_{10}Y = 0.645 \log_{10}X + 0.323$, where $n = 20$ and $r = 0.94$.

Table 2

Ratios of the aerial oxygen consumption of gastropods soon after emersion to that of animals subjected to a period of desiccation; ratios for the species in the present study are calculated after 4 h desiccation (20% RH) at 10°C for comparison with those reported by SANDISON (1966) after 3 h drying at 18°C and by BALDWIN (1968) after 3 h drying at 22°C; the principal respiratory organ of each species is indicated; NS denotes no significant difference between desiccated (after drying overnight) and undesiccated rate.

Species	Principal respiratory organ	Ratio of oxygen consumption	Reference
<i>Notoacmea pileopsis</i>	bipectinate gill	1:0.32	present study
<i>Collisella scabra</i>	bipectinate gill	1:0.43	BALDWIN (1968)
<i>Collisella digitalis</i>	bipectinate gill	1:0.25	BALDWIN (1968)
<i>Cellana radians</i>	pallial gills	1:0.76	present study
<i>Littorina saxatilis</i>	unipectinate gill	1:0.72	SANDISON (1966)
<i>Littorina littorea</i>	unipectinate gill	1:0.40	SANDISON (1966)
<i>Littorina obtusata</i>	unipectinate gill	1:0.38	SANDISON (1966)
<i>Nucella lapillus</i>	unipectinate gill	1:0.52	SANDISON (1966)
<i>Littorina irrorata</i>	unipectinate gill	NS	SHIRLEY <i>et al.</i> (1978)

Seawater $\log_{10} Y = 0.559 \log_{10} X + 0.511$, where $n = 21$ and $r = 0.83$.

The correlation coefficients for the aerial and aquatic regression analyses are both significant ($P < 0.05$). Analysis of covariance revealed no significant differences in either slope or elevation between the rates of oxygen consumption determined in air and seawater. The aquatic to aerial ratio for a standard weight animal (200 mg) is 1:0.97 at 10°C.

Effect of Desiccation on Aerial Oxygen Consumption

Aerial rates of oxygen consumption of *Notoacmea pileopsis* after 1, 4, and 8 h desiccation are all significantly lower ($P < 0.001$) than rates determined for limpets that had experienced a brief period of aerial exposure (Figure 3). The rates measured after 1 and 4 h desiccation are also significantly different ($P < 0.05$). The aerial oxygen consumption of *Notoacmea* decreases by over 50% at all three levels of desiccation—1 h (51%), 4 h (68%), and 8 h (57%).

The aerial oxygen consumption of *Cellana radians* decreases significantly after 1 h ($P < 0.001$), 4 h ($P < 0.05$), and 8 h ($P < 0.01$) desiccation compared to limpets after a brief period of aerial exposure (Figure 3). There are no significant differences between the rates after 1, 4, and 8 h desiccation. Decreases in the aerial oxygen consumption of *Cellana radians* after 1 h (36%), 4 h (24%), and 8 h (32%) desiccation are less than those reported for *Notoacmea pileopsis*.

DISCUSSION

In terms of its respiration in air and water, the acmaeid limpet *Notoacmea pileopsis* is an exception to the pattern of depressed rates of aerial oxygen consumption previously described for prosobranch limpets possessing primitive aspidobranch gills (BALDWIN, 1968; HUGHES, 1971a;

McMAHON & RUSSELL-HUNTER, 1977). The distribution of *Notoacmea pileopsis* may be compared with that of some neritids (HUGHES, 1971b; LEWIS, 1971; COLEMAN, 1976; HOULIHAN, 1979) and trochids (MICALLEF, 1967; MICALLEF & BANNISTER, 1967; HOULIHAN & INNES, 1982a, b) which also retain a bipectinate ctenidium and are subjected to long periods of aerial exposure.

The pattern of respiration in air and water for a number of acmaeid limpets (Table 1) seems somewhat similar to that described in comparative studies of trochids (MICALLEF, 1967; MICALLEF & BANNISTER, 1967; HOULIHAN & INNES, 1982a, b), *i.e.*, high shore species maintain aerobic metabolism during emersion while their low shore counterparts have reduced rates of oxygen consumption in air. Increased vascularization of the mantle (DESHPANDE, 1957; FRETTER & GRAHAM, 1962) may enhance aerial oxygen uptake in some high shore trochids (NEWELL, 1973) but it is not clear whether *Notoacmea* possesses any structural adaptations to promote aerial gas exchange.

The ratio of aquatic to aerial oxygen consumption of *Notoacmea pileopsis* is very similar to that of the patellid limpet *Cellana radians* (Table 1) whose oxygen uptake did not change significantly between aquatic and aerial environments at 10°C (Figure 2). Patellid limpets, whose principal respiratory organs are secondary pallial gills (PURCHON, 1968), generally appear well adapted for aerial oxygen uptake (Table 1), although aquatic to aerial ratios vary with size and temperature and may be modified to meet the overall energy balance of individual species (BRANCH & NEWELL, 1978; BRANCH, 1979; NEWELL & BRANCH, 1980).

The patterns of aerial oxygen consumption displayed by *Notoacmea pileopsis* and *Cellana radians* immediately after emersion and after periods of desiccation are remarkably similar (Figure 3). The oxygen uptake of both species decreased significantly after a relatively short (1

h) period of desiccation, and remained relatively constant during subsequent drying. It therefore appears that prosobranch limpets have two levels of aerial oxygen consumption: (1) a rate immediately on emersion (in this instance similar to the aquatic rate) and (2) a depressed rate indicative of desiccation stress (COLEMAN, 1976).

The decrease in aerial oxygen consumption of *Notoacmea pileopsis* after a period of desiccation is very similar to that reported for other acmaeids (BALDWIN, 1968), and the vertical range of this limpet does not appear to be correlated with any adaptations to minimize the respiratory effects of drying (Table 2). With the reservations that Table 2 contains limited data and comparisons are made using gastropods of different size ranges (WOLCOTT, 1973) there is some indication of a correlation between the principal organ of gas exchange and the effect of desiccation on aerial oxygen uptake. Desiccation appears to have a greater effect on the oxygen uptake of acmaeid limpets (BALDWIN, 1968; present study) than that of limpets possessing pallial gills (present study) or other prosobranchs with modified respiratory organs (SANDISON, 1966; SHIRLEY *et al.*, 1978).

The greater decrease in oxygen uptake during desiccation reported for acmaeids (Figure 3; Table 2) may involve the production of mucus slowing down both water loss (WOLCOTT, 1973) and oxygen uptake. In addition, the gill filaments may clump together during drying to occlude a large area of the respiratory surface.

The depressed rates of aerial oxygen uptake reported for *Notoacmea pileopsis* and *Cellana radians* during desiccation may conserve energy during aerial exposure (BRANCH & NEWELL, 1978; BRANCH, 1979; NEWELL & BRANCH, 1980). The desiccated rates in both instances are, however, significantly lower than the resting aquatic rate, and, if aerobic metabolism in air were to fall below the minimum maintenance level (NEWELL, 1979), then anaerobic metabolism may become important (BAYNE *et al.*, 1976; WIESER, 1980).

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